

Decomposition patterns of leaf litter of seven common canopy species in a subtropical forest: dynamics of mineral nutrients

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Abstract: Dynamical patterns of mineral elements during decomposition processes were investigated for seven common canopy species in a subtropical evergreen broad-leaved forest by means of litterbag technique over 2 years. The species studied are representative for the vegetation in the study area and differed significantly in chemical qualities of their litter. No significant relationships were found between decomposition rate (percentage dry mass remaining and decomposition constant k) and initial element concentrations. However, there were significant correlations between the percentage of dry mass remaining and the mineral element concentrations in the remaining litter for most cases. The rank of the element mobility in decomposition process was as follows: Na = K > Mg \geq Ca > N \geq Mn \geq Zn \geq P > Cu $>>$ Al $>>$ Fe. Concentrations of K and Na decreased in all species as decomposition proceeded. Calcium and Mg also decreased in concentration but with a temporal increase in the initial phase of decomposition, while the concentrations of other elements (Zn, Cu, Al, and Fe) increased for all species with exception of Mn which revealed a different pattern in different species. In most species, microelements (Cu, Al, and Fe) significantly increased in absolute amounts at the end of the litterbag incubation, which could be ascribed to a large extent to the mechanism of abiotic fixation to humic substances rather than biological immobilization.

Keywords: Canopy species; Element release; Litter decomposition; Litterbag experiment; Microelement; Evergreen broad-leaved forest

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Introduction

Nutrient release in litter decomposition is an important process in nutrient recycling in terrestrial ecosystems (Swift *et al.* 1979). Thus, litter decomposition influences primary productivity, net ecosystem carbon storage, and soil humus formation. A thorough understanding of decomposition processes is essential in understanding the structure and function of terrestrial ecosystems. Plant nutrients are released from litter by both physical leaching and breakdown of structural organic components by soil organisms. Nutrient dynamics in decomposing litter has been studied for many species (e. g. Berg *et al.* 2003; Gosz *et al.* 1973; Laszkowski *et al.* 1995; Xu *et al.* 2004b). Because different patterns were observed for the dynamics of particular chemical elements in various forest ecosystems, it was hypothesized that nutrient dynamics depended to a large extent on the nutrient availability to decomposers (Swift *et al.* 1979; Staaf *et al.* 1982). Nutrients limiting to decomposers would be accumulated during the initial phases of decomposition, while those exceeding the needs of decomposers could be released from the litter from the start of decomposition.

The emphasis in many decomposition studies has traditionally been on the dynamics of nitrogen, which most commonly limits forest growth in different ecosystems (Kimmens 2003). The dy-

namics of other elements, particularly microelements, have received less attention despite the well-proven impact on decomposition processes by some heavy metals as pollutants (Bengtsson *et al.* 1988; Coughtrey *et al.* 1979; Laskowski *et al.* 1995). The existing data are, however, so incomplete that no general model describing release dynamics of nutrients has been suggested up to date (Palviainen *et al.* 2004). More studies are required, since critical nutrient levels appear to vary with the system, and chemical litter quality in the same species may vary with years and locations. The mechanisms determining the dynamics of nutrients during litter decomposition are still poorly understood.

The subtropical evergreen broad-leaved forests in Okinawa have high tree species richness and are subject to frequent typhoon disturbances and monsoonal winds that typically structure lower stature forest (Itô 1997; Xu *et al.* 2001). It is notable that many tropical elements are abundantly represented in this forest, such as tree ferns, and littoral plants. There are over thirty endemic and endangered plant species growing in the forests (Hirata *et al.* 2001). Therefore, sustainable management and conservation of those forests is a prerequisite. Up to date, some studies have been conducted in this forest, but are mostly on forest management and vegetation structure and classification (Hirata *et al.* 2001). Those studies contribute a lot to our current understanding of this subtropical forest. However, little attention has been given to the pattern of nutrient cycling which is the basic function of forest ecosystem. In this forest, leaf litter contributed 60%-70% of the total fine litterfall (Xu *et al.* 2003; 2004c), and decomposition and nutrient mineralization of those leaves are key components of nutrient cycling. Although the decomposition process has frequently been studied in forest ecosystems, data on the decomposition process of litter in subtropical environment are few. More intensive studies and data set are necessary for a better understanding of decomposition proc-

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esses. The main objectives of this study were to determine the differences in patterns of mineral nutrient release between major canopy species and to analyze the relationships between initial litter quality and the release of nutrients in a subtropical forest ecosystem. Nevertheless, N and P dynamics during decomposition processes for those tree species have been reported by Xu and Hirata (2004a).

Study area and methods

Study area

This study was conducted at Yona Experimental Forest of the University of the Ryukyus, located in the northern part of Okinawa Island, southwestern Japan ($26^{\circ}45'N$ and $128^{\circ}10'E$). The area is characterized by a subtropical climate and abundant rainfall throughout the year. Annual mean temperature is about $21.8^{\circ}C$. Annual mean rainfall is 2 680 mm over last 30 years. (experimental forest, University of the Ryukyus). Mean annual relative humidity reaches 82%. Typhoons frequently occur between June and October. Monsoons, from the south or southwest, bring a rainy season between spring and early summer, and from the north or northwest create a relatively dry season in winter.

The topography of the area is hilly, and a mountain range runs from the northeast to the southwest in the center of the northern part of the Island. The highest peak, Mt. Yonaha is 498 m asl. Deep valleys dissect the area and steep slopes predominate. The bedrock is composed of tertiary sandstone and palaeozoic clay-slate except for a narrow area of palaeozoic limestone along the coastline where a yellow soil has developed (Kojima 1980). The mountainous landscape is covered with orange plantations and a wide range of forest ecosystems. Most of the lower slopes once covered by subtropical forest have also been converted to orange and pine plantations (Kojima 1980; Yamamori 1994). This experimental forest is dominated by a secondary forest that was harvested for fuelwood, particularly for charcoal production

during the Second World War; and the forest had not been logged or thinned afterward (Hirata, pers. comm. 2004). The forest is characterized by short canopy with a dense understory. In this forest, there are approximately 50–70 tree species per hectare (over 3 cm DBH), and the taxonomic families most frequently represented are the Fagaceae, Theaceae, Lauraceae, and Aquifoliaceae (Xu et al. 2001). The experimental plot situated in hilly terrain on an upper slope (26°) facing $N65^{\circ}W$ at an altitude of 260 m asl. Trees with DBH greater than 3.0 cm were found at a density of 6600 stems·hm⁻². The total basal area was 45 m²·hm⁻². The soil at study site has a clay loam texture, and has developed from Palaeozoic clay-slate. Soil pH (H₂O) is 4.1. Concentrations of total organic C and total N are 62.5 and 3.8 g·kg⁻¹. Available P is 18.2 mg·kg⁻¹. Exchangeable cations are: K⁺ 0.31, Ca²⁺ 2.83, Mg²⁺ 1.34 cmol·kg⁻¹, respectively, in the top of 10-cm mineral horizon. This soil type corresponds to a Typic Paleudults according to the USDA classification (Soil Survey Staff 1999).

Materials

Decomposition rates of leaf litter were measured for seven major canopy species: *Castanopsis sieboldii* Hatusima ex Yamazaki et Mashiba (Cs), *Quercus miyagii* Koidz. (Qm), *Schima wallichii* Kort. (Sw), *Symplocos confusa* Brand (Sc), *Daphniphyllum glaucescens* Bl. (Dg), *Distylium racemosum* Sieb. et Zucc. (Dr) and *Rapanea nerifolia* Mez. (Rn). Litterfall from those species contributed over 85 % of the total fine litterfall (Xu et al. 2004c). The leaf litter for decomposition experiment was collected with litter traps at same plot during the peak of leaf fall in March 1998 and 1999 since leaf litterfall in this month contributed about half of the annual total leaf litter. The litter collected was oven-dried at 70°C, then sealed in polythene bags and preserved below 15°C in the laboratory. The chemical composition of the leaf litter in the species is given in Table 1. Nomenclature follows Hatushima and Amano (1994).

Table 1. Initial chemical composition of leaf litter from species in a subtropical forest in Okinawa (mg·kg⁻¹ for Fe, Zn and Cu; g·kg⁻¹ for the other elements)

Species	N	P	K	Ca	Mg	Al	Na	Mn	Fe	Zn	Cu
<i>C. sieboldii</i>	9.29c (0.57)	0.23c (0.03)	3.08d (0.18)	7.72c (0.54)	2.59d (0.13)	1.12c (0.31)	1.52bc (0.38)	0.44a (0.03)	90.1a (5.11)	6.18e (0.47)	3.72bc (0.29)
<i>D. glaucescens</i>	12.66a (0.79)	0.31ab (0.05)	3.45d (0.40)	9.38b (1.17)	5.81a (0.27)	1.03c (0.21)	1.20c (0.25)	0.14d (0.02)	61.4d (3.96)	13.67b (1.19)	4.96a (0.27)
<i>D. racemosum</i>	5.46f (0.44)	0.14d (0.05)	1.76e (0.33)	12.55a (1.07)	3.41c (0.18)	0.38d (0.07)	0.94d (0.13)	0.44ab (0.11)	50.5e (3.47)	10.33c (1.05)	2.97dc (0.13)
<i>Q. miyagii</i>	8.08d (0.71)	0.14d (0.05)	2.47c (0.27)	6.08e (0.67)	1.73f (0.11)	0.25e (0.09)	0.96d (0.06)	0.42ab (0.07)	78.9bc (4.77)	13.23b (0.99)	3.32c (0.15)
<i>R. nerifolia</i>	7.03e (0.46)	0.16d (0.03)	1.32f (0.16)	11.05b (0.52)	2.14e (0.03)	0.13f (0.03)	1.85ab (0.28)	0.35b (0.03)	76.3bc (5.01)	7.37d (0.52)	3.48bc (0.15)
<i>S. confusa</i>	9.24c (0.93)	0.32a (0.04)	4.87a (0.29)	6.75d (0.33)	3.99b (0.24)	3.04a (0.27)	1.01cd (0.18)	0.25c (0.01)	80.2b (5.09)	16.61a (1.22)	3.02dc (0.13)
<i>S. wallichii</i>	10.16b (0.77)	0.21c (0.04)	4.35b (0.29)	8.18c (0.82)	2.46d (0.15)	1.53b (0.33)	2.11a (0.41)	0.51a (0.04)	72.6c (4.18)	6.51de (0.53)	4.03b (0.21)

Notes: Values are means with S.D. in the parentheses (n = 4). Values with the same letter in a column are not significantly different (Tukey multiple comparison test; $p > 0.05$).

Litterbag experiment

Litter decomposition studies were carried out by using the litterbag technique (Bocock et al. 1960). Litter bags (20 cm × 15 cm) were made of 1-mm polyester mesh. Before the experiment, four subsamples from the respective litter samples were taken to

determine moisture and initial chemical concentrations. The equivalent of 10 g of dry litter was sealed in each bag. Eighty litterbags per species were randomly placed in six blocks on the soil surface at the study site used for litterfall studies. The experiment, lasting 2 years, started on 6 July 1999. Collections

were made every month in the first 6-month period, and then they were made in 3-month intervals. Six replicate litterbags were sampled at each time. After removal of the soil and other extraneous materials, the bagged litter samples collected were oven-dried within 24 h at 70 °C to a constant weight, and then milled for chemical analysis.

Chemical analysis

The subsamples (the ground samples) of 1.0 g each were digested with HNO₃-HClO₄ reagent, and analyzed for the concentrations of K, Ca, Mg, Na, Al, Fe, Mn, Cu and Zn by inductively coupled plasma spectrometer (Shimadzu, ICPS-2000, Kyoto, Japan). The procedure for nutrient analysis followed the Editorial Committee of Experimental Methods for Plant Nutrition, Japan (1990).

Statistical analysis

There were six replicates for each litter type and all litterbags were randomly selected for collection. All data were analyzed by Statistica (StatSoft, Japan Inc. 1999). Single variable regressions were used to correlate decomposition rates with the initial element concentrations of the litter. Differences in substrate chemistry between species were tested using one-way analysis of variance (ANOVA). The multiple comparisons were made using Student-Newman-Keuls test. In all analyses, $P < 0.05$ was the criterion for significant differences.

Results

Weight loss

The dry mass remaining among studied species after two years varied significantly in an order of magnitude: *D. racemosum* > *Q. miyagii* > *R. neriifolia* > *S. confusa* > *C. sieboldii* > *S. wallichii* > *D. glaucescens*. After 2 yr., *D. glaucescens* leaf litter was decomposed completely whereas that of *D. racemosum* had lost only 45.6% of its initial dry weight. A rapid initial phase of mass loss was observed for all species measured (Fig. 1a). Much mass loss occurred in *D. glaucescens* litter after the first 3 months when 44.8% of its original dry mass was lost, by comparison only 26.5% mass lost in *D. racemosum* litter.

Potassium and sodium

The initial concentration of K was highest in *S. confusa* and lowest in *R. neriifolia*, while Na was highest in *S. wallichii* and lowest in *D. racemosum*. The result from the present study showed that K and Na were subject to extensive leaching from litter in decomposition. Mass loss was rapid in the first month, and was very low afterwards. The initial masses of K and Na in different species were lost by 73%–98% and 69%–88%, respectively, during the first months. No significant difference appeared among species (Fig. 1b and 1c).

Magnesium and calcium

The highest initial concentrations of Ca and Mg were found in *D. racemosum* and *D. glaucescens*, respectively, while the lowest ones of both Ca and Mg were in *Q. miyagii*. The release of Ca and Mg was somewhat rapid during study period, especially in the first year, in which 40%–80% of their initial masses were lost. No difference appeared in the patterns of Mg release amongst species (Fig. 1d). However, Ca release in *D. racemosum* was considerably low in the first year, compared with that of the

other species (Fig. 1e).

Aluminium and iron

The initial concentrations of Al varied mostly among species. The highest concentration was found in *S. confusa* (3.04 mg·g⁻¹), which was about 23-fold as high as in *R. neriifolia*. Significant accumulations of Al and Fe were found in the present study (Fig. 1f and 1g). Dynamical patterns for Al in decomposition varied significantly amongst species. Based on the immobilization of Al during the decomposition process, the species measured could be divided into two groups, i.e. high and low Al accumulation species. However, no significant difference appeared for the pattern of Fe in the early stage (the first year), but in the late stage significant differences occurred. *D. racemosum* showed to be great immobilization of Fe in decomposition.

Manganese

The initial concentration of Mn varied in a range of 0.14–0.51 mg·g⁻¹ among the species. All species demonstrated significant net accumulation (120%–209% of the initial mass) of Mn in the first year decomposition. Afterwards the rapid loss of Mn occurred in all species, (Fig. 1h). After 2-yr. decomposition, net accumulation of Mn was observed only in *Q. miyagii* and *S. confusa* (30% and 40% of their initial masses, respectively).

Copper and zinc

The initial concentrations of Cu and Zn varied in 2.97–4.96 mg·kg⁻¹ and 6.38–16.61 mg·kg⁻¹, respectively, among species. After 1-yr decomposition, significant net accumulation of Cu and Zn was observed in all species except for *D. glaucescens* that showed a stable release from the beginning of the decomposition experiment (Fig. 1i and 1j). After 2-year decomposition, only two species, *R. neriifolia* and *D. racemosum* showed net accumulation of Zn. However, both *D. glaucescens* and *S. wallichii* showed net release of Cu. The results indicated that the mobility of Zn was higher than that of Cu during decomposition of leaf litter.

Discussion

Initial litter quality and nutrient dynamics

Litter quality (mainly C and N) appears to regulate decomposition processes (Berg *et al.* 2003). The previous report from Xu and Hirata (2004a) showed that the initial N concentration, and lignin:N and C:N ratios are good predictors of decomposition rate for the overall 2-year decomposition. In this study, no significant relationships were found between decomposition rate (percentage dry mass remaining and decomposition constant *k*) and initial element concentrations (data not shown). For most presented cases, however, there were highly significant correlations between the percentage dry mass remaining and the mineral element concentrations in the remaining litter (Table 2).

The release pattern of K and Na in decomposing leaf litter was distinctly different from that of other elements. Loss of K and Na was immediate and rapid in the first months. Thereafter, the loss rate of K and Na declined slightly. Both K and Na are usually reported as having the highest release rates in a broad range of forest ecosystems (e.g. Enright *et al.* 1987; Laskoweski *et al.* 1995; Xu *et al.* 2004b). This pattern is characteristic of K and Na (Gosz *et al.* 1973) since they are not the structural component of plant litter and are subject to physical removal by leaching with-

out microbial activity (Tukey 1970).

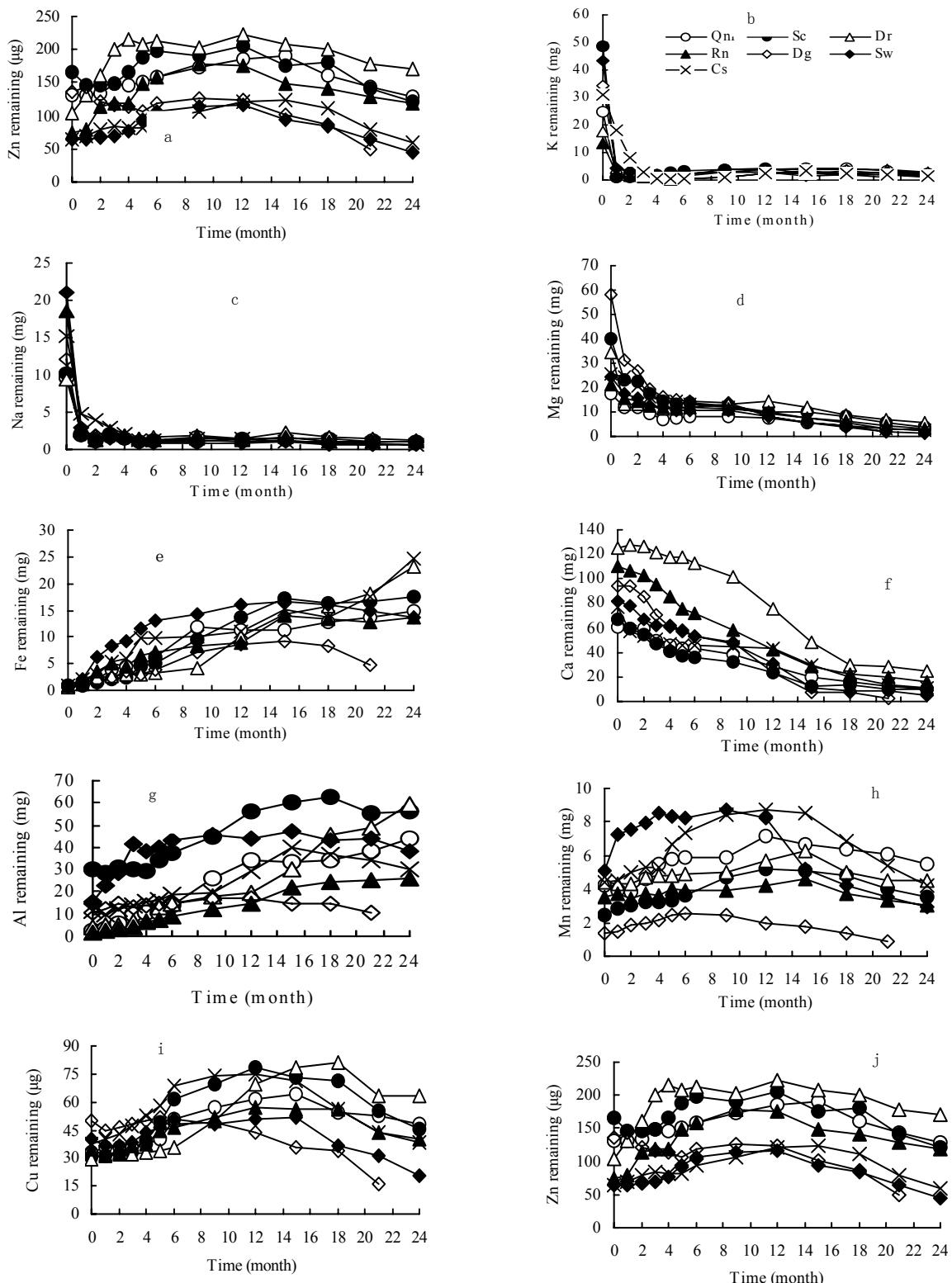


Fig. 1 Changes in (a) dry mass and (b - j) element amount remaining per litterbag in seven canopy species during decomposition processes in a subtropical forest. Abbreviations in the figure are: Cs, *Castanopsis sieboldii*; Dg, *Daphniphyllum glaucescens*; Dr, *Distylium racemosum*; Qm, *Quercus miyagii*; Rn, *Rapanea nerifolia*; Sc, *Symplocos confusa*; Sw, *Schima wallichii*.

The pattern of Ca release was similar to that of the dry matter loss because Ca was a structural component. Thus Ca was pro-

tected from physical leaching (Gosz *et al.* 1973; Edmonds *et al.* 1995). In the present study, the dynamic pattern was similar with

a net release in all species except for *D. racemosum* that had a slightly accumulation in the initial phase of decomposition (Fig. 2e). Previous studies demonstrated that Ca dynamics patterns during litter decomposition showed either increase-decrease phases (Berg *et al.* 1987; Edmonds *et al.* 1995; Klemmedson *et al.*

1985; Kalburjji *et al.* 1999) or a decrease phase only (Adams *et al.* 1996; Edmonds 1984; Xu *et al.* 2004b). The mechanism behind such dynamic patterns could be related directly to the organic matter decomposition rate, and the demand of Ca in decomposer organisms (Fahey 1983; Laskowski *et al.* 1995).

Table 2. Results of the regression analysis on relationship between percentage litter mass remaining and element concentrations in the remaining litter (significant levels: *, P<0.05; **, P<0.01; *, P<0.001)**

Elements	<i>C. sieboldii</i>	<i>D. glaucescens</i>	<i>D. racemosum</i>	<i>Q. miyagii</i>	<i>R. neriifolia</i>	<i>S. confusa</i>	<i>S. wallichii</i>
K	0.452*	0.503**	0.311	0.121	0.112	0.491**	0.343*
Na	0.542**	0.521**	0.557**	0.335*	0.511**	0.519**	0.407*
Ca	0.546**	0.405*	0.299	0.499**	0.481**	0.478**	0.617**
Mg	0.887***	0.931***	0.563**	0.824***	0.683***	0.879***	0.858***
Al	0.829***	0.881***	0.593**	0.738***	0.722***	0.690***	0.925***
Mn	0.755***	0.734***	0.738***	0.885***	0.830***	0.740***	0.415*
Fe	0.764***	0.694***	0.580**	0.777***	0.787***	0.626**	0.913***
Zn	0.771***	0.714***	0.697***	0.819***	0.809***	0.697***	0.756***
Cu	0.778***	0.628**	0.633**	0.803***	0.769***	0.616**	0.732***

The dynamical patterns of Mg observed in the present study were some different from those of Ca, with somewhat rapid release in the initial phase (Fig. 2d). Despite of the release of Mg from the start of decomposition, its concentration decreased slightly, implying a linear relation between Mg dynamics and litter decomposition. Staaf and Berg (1982) reported a similar result. Thus, the mechanisms described for Ca can be suggested as controlling the dynamics of Mg as well (Laskowski *et al.* 1995).

The greatest net accumulation in decomposition process was found for Fe and Al in the present study. After 2-yr. decomposition, no net release of both Fe and Al occurred in all species except for *D. glaucescens* that decomposed completely over 2 years. The increase in concentrations and amounts of Al and Fe, during litter decomposition in the present study, is not a rare observation (Gosz *et al.* 1973; Laskowski *et al.* 1993; Laskowski *et al.* 1995; Palviainen *et al.* 2004). The accumulation of heavy metal ions such as Al and Fe during decomposition process is ascribed to an abiotic formation of highly stable complexes with humic substances (Rustad *et al.* 1988) or to a biotic accumulation in decomposer microorganisms (Cromack *et al.* 1975; Stevenson 1982; Tate *et al.* 1995). These nutrients are finally mineralized in the very late stages (Rustad *et al.* 1988).

During litter decomposition, Mn is thought to be less mobile as Mg and Ca in many cases (Lousier *et al.* 1978; Edmonds *et al.* 1995). In the present study, Mn dynamics was noted to form an increase-decrease phases for most species. However, a net increase in Mn mass was also observed in *Q. miyagii* and *S. confusa* (Fig. 2g). Gosz *et al.* (1973) reported a decrease in Mn as decomposition proceeds. It is unclear what kind of biological mechanisms could be responsible for Mn dynamics (Laskowski *et al.* 1995). The accumulation of Mn in decomposing litter could be due to microbial immobilization and even transport by fungal mycelium from mineral soil (Berg *et al.* 1991), and an addition from exogenous sources (Lousier *et al.* 1978).

The dynamical patterns of Zn and Cu in decomposition were somewhat similar to those of Mn with an increase-decrease phases, while Cu had a low accumulation rate in the initial phase and a low release rate in late phase of decomposition compared to that of Zn in all species. It indicates that Cu can be firmly coagulated or chelated by organic matter (Rustad *et al.* 1988). On the other hand, Cromack *et al.* (1975) and Berg *et al.* (1991) found accumulation of some heavy metals (including Cu, Fe, Al

and Zn) in litter fungi, and this might suggest that some biological processes could be also involved in the dynamics of heavy metals in decomposition process.

Mobility of chemical elements during decomposition

In term of release rates, the average ranks of the element mobility in decomposition process could be ordered as follows: Na = K > Mg \cong Ca > N \cong Mn \cong Zn \cong P > Cu >> Al >> Fe. The range of ranks for an individual element in different species usually did not exceed 3 on a scale of 11 above-mentioned orders, suggesting that the release or accumulation of chemical elements in decomposition processes was controlled in a similar manner regardless of different species. This order may suggest the great importance of purely chemical interactions occurring in litter to the mobility of most metals (Laskowski *et al.* 1995). The above-mentioned order coincides with that of ordering metal ions by the decreasing stability of complexes with humic and fulvic acids (Stevenson 1982): $\text{Na}^+ > \text{K}^+ > \text{Mg}^{2+} > \text{Ca}^{2+} > \text{Mn}^{2+} > \text{Zn}^{2+} > \text{Cd}^{2+} > \text{Pb}^{2+} > \text{Cu}^{2+} > \text{Al}^{3+} > \text{Fe}^{3+}$. Results from regression analysis demonstrated that the variation in element concentrations during decomposition was correlated significantly each other particularly between heavy metals (Fe, Al, Cu, Mn and Zn) in all species, but with an exception of K and Na that had no significant relations to other elements (data not shown). This implies that between-elements interaction relating to the mobility occurred in decomposition processes.

In conclusion, the results of this study demonstrated that the dynamical patterns of nutrients during decomposition varied among both species and nutrients with respect to both the mobility of nutrients and limitations of nutrients on decomposer organisms (Berg *et al.* 2003). The dynamics of nutrients in decomposition process could be controlled by three major factors, i.e. physical, biological and chemical factors. The physical factor was dominated by leaching including K, Na and organic matter in the present study. The biological factor was dominated in dynamics of N, P, Mg, and Ca. Those chemical elements particularly N and P could be the limiting factors for the growth of decomposer population and immobilized by litter microorganisms (Swift *et al.* 1979; Vitousek *et al.* 1994). The chemical factor seems dominated by ion-bonding processes of humic substances produced as secondary compounds during litter decomposition. This should be the main mechanism responsible for the accumulation of Al, Fe and Cu in the present study despite of some bio-

logical processes involved (Cromack *et al.* 1975). The major nutrients (particularly for N and Ca in the present study) which dynamics are undoubtedly determined by biological processes increased only in their concentrations but not in their amounts during decomposition, and the heavy metals (Al, Fe and Cu) increased both in concentrations and absolute amounts in most species at the end of litter-bag incubation. This significant difference hints obviously that biological immobilization of heavy metals can be negligibly compared to the abiotic fixation to humic substances.

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